ON THE BLOOD VESSELS, THEIR VALVES AND THE COURSE OF THE BLOOD IN LUMBRICUS.[1]

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In a previous paper[2] an account has been given of the experimental study of the course of the blood flow in *Lumbricus* The most important result there set forth was that the circulation is not segmental but strictly systemic. The course of the flow is as follows : forward in the dorsal vessel for its whole length ; downward in the hearts ; both forward and backward from the hearts in the ventral vessel ; outward from the ventral to the body wall, nephridia and intestinal wall ; toward the lateral neurals from the body wall ; backward in the subneural ; upward to the dorsal vessel in the parietals from the subneural, the nephridia, and the body wall, and in the dorso-intestinals from the intestine. Thus, there is no circuit of blood in each segment to which a sytemic circuit for part of the blood has been superadded, as all previous authors have maintained, but all of the blood flows in a single systemic circuit. In the head region the blood is carried forward beyond the hearts by both dorsal and ventral vessels and is returned to the dorsal behind the hearts in larger part by the lateral œsophageals, and in smaller part by the subneural and the parietals of XII. and succeeding somites. The lateral œsophageal system is considered to represent the parietals in the somites anterior to XII.

This view of the circulation raised two important questions which further work has answered : (1) What happens when the hearts are removed from the circulation by decapitating the worm? Do the conditions which obtain in the regenerating

[1] Studies from the Zoölogical Laboratory of West Virginia University, No. 8, February 28, 1903. A part of the work reported here was done by my former student, Miss S. W. Johnson. For the conclusions reached the present writer alone is responsible.

[2] "The Course of the Blood Flow in *Lumbricus*," by J. B. Johnston and Sarah W. Johnson, *Amer. Naturalist*, April, 1902.

worm confirm the above results? (2) What is there in the structure of the blood vessels to determine and control the course of the blood?

The first question has been answered by a series of regeneration experiments carried out upon large and small specimens of *Lumbricus*. Operations removing from eleven to twenty somites from the anterior end were performed upon 171 worms. These were examined alive from time to time and eventually 20 were hardened for sectioning. The time that the worms were allowed to live varied from ten days to three and a half months. In a few worms regeneration progressed well, but the majority died after a few days or weeks. A detailed report upon these experiments would not be profitable for our present object. Although there were very great variations in the condition of the blood vessels, the following may be said to be true in greater or less degree of all the worms studied alive or sectioned. The vessels in the anterior one fourth to one half of the worm were greatly crowded and distended with blood. The anterior portion of the worm was usually a bright red to the naked eye and under a lens many small vessels not usually visible were distinctly seen. Sections showed that all the vessels were more or less crowded with blood, while the dorsal, subneural, and the vascular plexus of the intestinal wall showed the greatest distension. The ventral vessel was seldom stretched much beyond its normal size, while the subneural was often as great in diameter as the ventral. Occasionally the subneural was much larger than the ventral and sometimes its cross-section was equal to that of the nerve cord. In several cases the vascular layer of the intestine was very greatly crowded and, considering its great capacity in normal conditions, it is probable that it always held the greatest accumulation of blood. The posterior portion was very poor in blood in all worms.

These conditions are readily explained in accordance with the scheme of circulation above summarized. The fulness of the dorsal, intestinal and subneural vessels is due to the pressure from the dorsal which is deprived of the normal outlet for the blood carried by it, and forces the blood downward in the dorso-intestinals and parietals contrary to its usual course. The small

amount of blood in the ventral is due to the absence of the hearts and the inability of the dorsal to drive the blood through the capillary systems to the ventral. The absence of blood in the posterior end is a further result of the small amount of blood received by the ventral. If there were a segmental circulation in *Lumbricus* there would probably be no great accumulation of

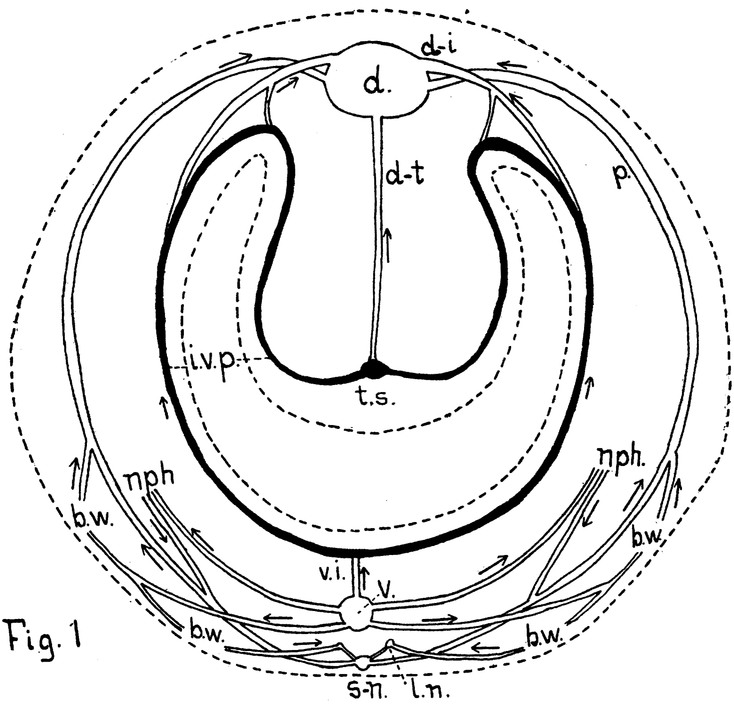

Fig. 1

FIG. 1. General scheme of circulation in body region, all the vessels of one segment being projected upon the plane of a transverse section. The vascular layer of the intestine is shown by a broad black line. In the typhlosole the vascular plexus thickens at one place to form the typhlosolar sinus which varies greatly in size in different worms and in different parts of the same worm. From this sinus three dorso-typhlosolar vessels in each segment carry blood to the dorsal vessel. These vessels and the branching of the dorso-intestinal vessels shown in this figure have not before been correctly described or figured for *Lumbricus*.

blood at the anterior end in these experiments, since the segmental circulation would tend to relieve the systemic and the even distribution of the blood would be maintained in accordance with the law of least resistance. These regeneration experiments,

therefore, seem to confirm the results of physiological experimentation. No effort was made to trace the development of hearts in the regenerated heads and the final reorganization of the circulation, and it is doubtful whether the worms would have lived long enough for this purpose.

It is probable that the failure of the blood vessels to adjust themselves to the new conditions is at least one of the chief causes of the death of worms under these experiments. The continued strong pulsations of the dorsal vessel after the removal of the hearts force the blood out through vessels which normally empty into it. In some cases the reversal of flow through the vessels of the body wall and intestines is produced readily enough to allow the worm to survive the operation, but in most cases less blood would reach the ventral vessel than is necessary to supply the posterior end of the worm and an insufficient amount of blood would pass through the respiratory plexus beneath the hypodermis. The blood which leaves the dorsal vessel in the anterior part of the worm either settles in the vascular layer of the intestine, which readily expands to receive it, or passes directly through the parietals to the subneural, which is consequently greatly expanded; and avoids the respiratory plexus because of the resistance in that quarter. A similar withdrawal of blood from the respiratory plexus of the posterior end of the worm also results indirectly from the small amount of blood in that region, so that the whole worm is seriously deprived of needed oxygen. In the normal circulation the blood is driven to the respiratory plexus from the ventral under direct pressure from the hearts, and there is no other way of less resistance by which the blood may return from the ventral to the dorsal. Upon the view of the circulation held by Bourne[1] and Harrington,[2] namely, that the dorso-intestinals empty into the dorsal vessel and the parietals carry blood away from it, it is evident that the path of least resistance from the pulsating dorsal vessel is through the parietals directly to the subneural and that there would be nothing to drive the blood through the respiratory

[1] Bourne, A. C., "On *Megascolex cœruleus* and a Theory of the Course of the Blood in Earthworms," *Q. J. M. S.*, Vol. 32, p. 49, 1891.

[2] Harrington, N. R., "The Calciferous Glands of the Earthworm, with an Appendix on the Circulation," *Jour. Morph.*, Vol. 15, Suppl., p. 105, 1899.

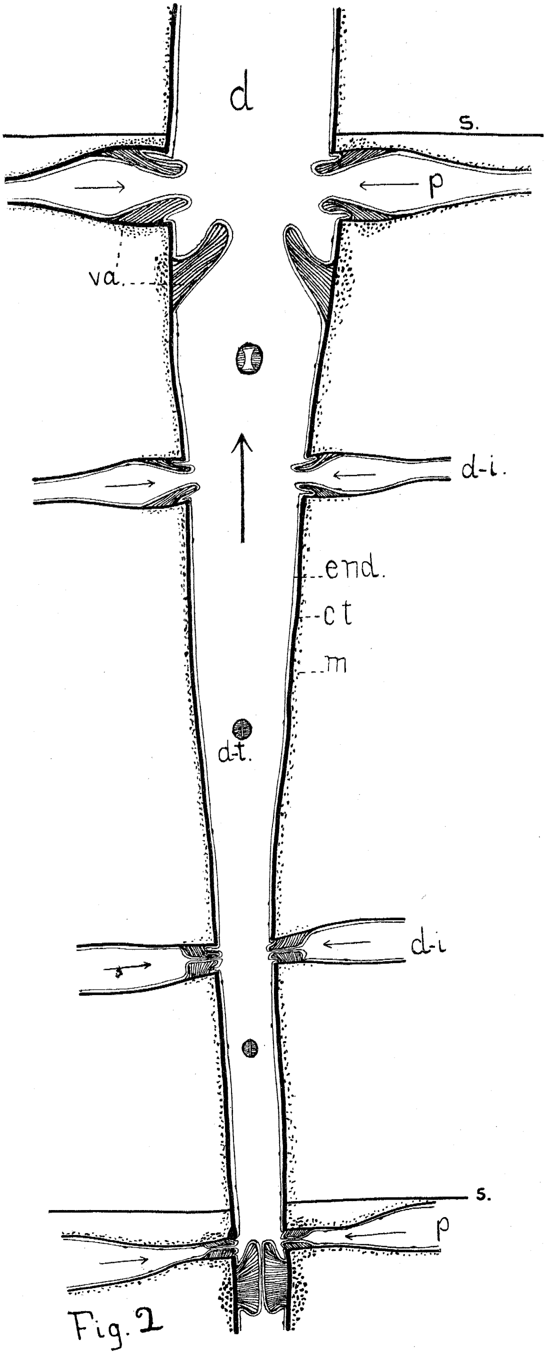

FIG. 2. A diagrammatic horizontal section of the dorsal vessel and those emptying into it. One somite and part of a second are shown, and the last part of a pulse wave and the greater part of a following contraction wave are represented. The arrows show the course of the blood and the position and changes of form of the valves are shown. The chloragogue cells covering the walls of the vessels are not drawn.

capillaries of the body wall. This is perhaps an insuperable objection to that theory of the circulation. This objection does hold against the view of Perrier[1] and Benham,[2] according to which the blood flows to the dorsal vessel in the parietals and out from it in the dorso-intestinals.

The study of the structure of the vessels shows that the movement of the blood is determined by the structure of the walls and by definite valves which several of the vessels possess. The wall of the dorsal vessel consists (Fig. 2) of a lining endothelium of very thin cells whose nuclei alone are usually visible; a connective tissue layer containing a few longitudinal (muscle?) fibers, and a well-developed layer of circular muscle fibers. Outside these are the chloragogue cells. To the layer of circular muscle fibers are due the pulsations of the dorsal vessel, and thickenings of this layer at certain points assist in the action of the valves, as will be described below. The wall of the ventral vessel has no circular muscle layer. Its lining endothelium is more conspicuous than that of the dorsal vessel and the connective tissue layer is very thick. This is a strong fibrous layer and gives great rigidity to the wall of the ventral vessel. Outside of the connective tissue layer are a few (4 to 6) strands of longitudinal fibers which take the same stain as the muscle fibers in the sheath of the neighboring nerve cord. Outside these fibers is a layer of peritoneum closely similar to that covering the inner surface of the body wall.

The subneural consists of only the endothelium and connective tissue layer, outside of which is the sheath of the nerve cord. This is the structure of the lateral neurals also, and of all the smaller vessels. The dorso-intestinals and parietals present an intermediate condition between those with and those without a circular muscle layer. The dorso-intestinal vessels are devoid of muscle fibers except at their dorsal ends where there is a thin extension of the circular layer of the dorsal vessel for a short distance. The parietals are provided with a thick band of circular fibres close to their connections with the dorsal and the layer is

[1] Perrier, Edw., "Recherches pour servir à l'histoire des Lombriciens terrestres," *Nouv. Arch. du Mus. d'Hist. Nat.*, Paris, Tome 8, 1872.

[2] Benham, W. B., "The Nephridium of *Lumbricus* and its Blood Supply," *Q. J. M. S.*, Vol. 32, p. 293, 1891.

continued along the vessel for about a third or half its length. These muscle fibers in the dorsal portion of the parietals produce the active pulsations which have been described in an earlier paper (*loc. cit.*, p. 323).

The walls of the hearts have the same structure as that of the dorsal vessel, except that they are covered with chloragogue cells only in their dorsal portion, elsewhere by peritoneum. The circular muscle fibers are large and the layer somewhat stronger than that in the dorsal vessel.

The structure of the vessels determines whether they shall propel the blood by their pulsations or only carry it, and the account of the structure accords with the well-known facts concerning the pulsations of the vessels. Pulsations in the dorsal, parietals and hearts are well established; pulsations in other vessels, described by Harrington, have not been seen by the author and to whatever extent they occur they must be produced without muscle fibers.

Valves are present in the dorsal vessel and in all the vessels connected with it, namely, the dorso-intestinals, dorso-typhlosolars, parietals, lateral œsophageals (?) and hearts. The valves in the dorsal are a pair of large thick flaps attached to the lateral walls of the vessel at a point a short distance behind each septum and immediately behind the openings of the parietals. These valves are always directed forward and allow the free passage of blood during the pulse wave. As the contraction wave approaches, the valves are brought into contact and at the moment of greatest constriction the two flaps are tightly pressed together and completely close the lumen of the vessel. The efficiency of the valves is secured and increased by a considerable thickening of the circular muscle layer at the valve (Fig. 2). The valves do not act in the ordinary manner of flap valves, but the two fleshy flaps are pressed together and form a large mass which fills the vessel. In the region of the hearts a pair of valves is found in the dorsal vessel a short distance in front of each pair of hearts.

The valves in the dorso-intestinal, dorso-typhlosolar and parietal vessels are essentially the same in form and position. In each of these vessels (Fig. 2) a pair of small fleshy flaps are sit-

uated at the opening of the vessel into the dorsal. In the dorso-intestinal and parietal vessels the flaps are attached one to the anterior and one to the posterior wall of the vessel, and the body of the flap projects into the lumen of the dorsal vessel. In the dorso-typhlosolars the flaps are lateral in position, are situated deeper in the vessels, and do not project so far into the dorsal. It is evident that pressure from the dorsal toward any of these vessels would tend to close the valves. The closing of the parietals is further secured by a thickening of the circular muscle layer as in the dorsal; and in the dorso-intestinals a thin extension of the muscle layer of the dorsal serves the same purpose. Muscle fibers have not been observed in the dorso-typhlosolar vessels. The valves in these vessels allow the blood to flow from them into the dorsal only, and this accords with the results obtained by the earlier experimental investigation. In the case of the decapitated worms the valves in all these vessels near the anterior end must have been forced.

The hearts are better supplied with valves than are any of the other vessels. In each heart are four pairs of valves (Fig. 3); one situated close to the dorsal vessel, one between the first and second thirds from the dorsal end, one between the second and third thirds, and the fourth in the ventral end of the heart at the opening into the ventral vessel. The three pairs in the body of the heart are like those in the dorsal vessel but are smaller in proportion to the diameter of the heart. They are inclined downward and are large enough to close the heart during its contraction. The presence of these valves might seem unnecessary in view of the fact that the contraction waves pass along the heart from above downward. However, if from any cause the contraction becomes modified or irregular or if the whole heart contracts at once, the functional importance of these valves is evident. It is a matter of common observation that such irregularities in the contractions of both the hearts and the dorsal vessel do appear in worms dissected alive under an anæsthetic, and it is probable that such irregular contractions and the influence of movements of the body make necessary the valves in the hearts and the dorsal vessel in the normal worm. The valves in the smaller ventral ends of the hearts fill the lumen and project

into the ventral vessel very much as the valves in the parietals project into the dorsal. Thus, with the valves in the dorsal between each two pairs of hearts and the four valves in each heart, regurgitation of blood during the strong cardiac contractions is effectively guarded against.

The study of the fine structure of the valves has presented great difficulties because methods of fixation which give satisfac-

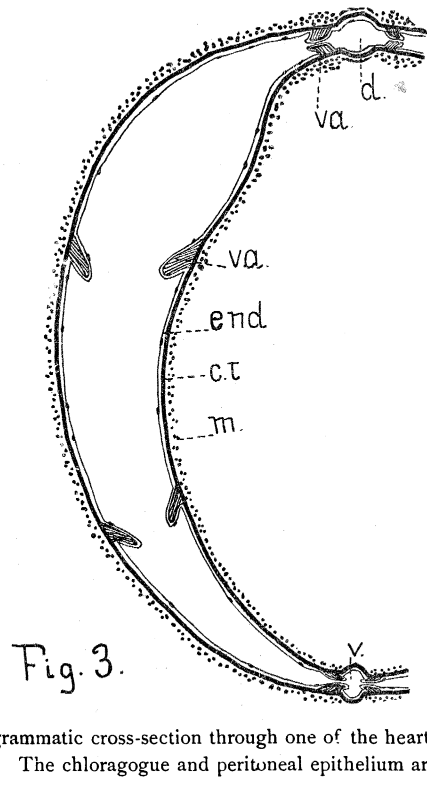

FIG. 3. A diagrammatic cross-section through one of the hearts to show the position of the valves. The chloragogue and peritoneal epithelium are not drawn.

tory preparations of all other tissues give very imperfect pictures of these valves. This itself indicates one fact regarding their structure, namely, that they are composed of very soft-bodied or watery cells which may appear vacuolated or shrunken, or even macerated. In many preparations the valves appear only as masses of granular or coagulated material containing many ovoid nuclei. In the most successful sections, however, the valves

show indistinct cell boundaries which produce an appearance of striations running from base to free edge of the valve. In most preparations, especially in longitudinal sections of the dorsal vessel, which are often oblique owing to the curves of the vessel, the substance of the valves appears to be sharply delimited from the connective tissue layer. This would indicate that the valve is formed by a thickening of the endothelial layer. It is difficult to disprove this first supposition because the endothelial cells are so broad that one can seldom expect to find an endothelial nucleus on the surface of a valve. However, in some cases in the hearts flattened nuclei similar to those of the endothelial cells are found on the surface of the valves. Cross-sections of the dorsal vessel through the base of the valves show a radial striation running from the valves through the connective tissue and muscle layers. From these facts it appears that the valves are composed of elongated cells which run through the connective tissue layer and securely anchor the valves. Since they are covered internally by endothelial cells they must be regarded as belonging to the connective tissue layer. Essentially the same structure is presented by all the valves, although those in different positions differ greatly in size and form in relation to the function which they have to perform. The largest valves are those in the dorsal vessel. These are thick flaps attached by broad bases to the lateral walls of the vessel. When the vessel is distended the valves are nearly semilunar in form. When the vessel is contracted the valves become greatly compressed against one another and the soft substance of the valve is forced both forward and backward from its point of attachment. When the valve extends far forward it overlaps the opening of the parietal vessel and might appear to function to close that vessel. Such a condition seems to have been seen by Benham (*loc. cit.*). The valves in the dorso-intestinal and parietal vessels are also paired flaps, but owing to the small size of the vessels the flaps are small at their bases and are longer than they are broad. Often these valves have a balloon form as they project into the dorsal vessel. The valves in the dorso-typhlosolar vessels are situated somewhat farther within the vessels and are more nearly simple semicircular flaps. The valves at the ventral ends of the hearts are relatively large

and project so far into the ventral vessel that they might be mistaken for valves proper to the ventral vessel itself.

The course of the blood flow is determined by the disposition of the valves as well as by the direction of the pulsations, and there is evidently entire agreement between the results of the physiological experiments and anatomical investigation. It is obvious that in small vessels or in such as receive blood from a capillary system so that there is no great pressure in the usual course, there may occur temporary reversals of flow due to movements of the body or other causes. Such reversals might most readily take place in the subneural vessel and such phenomena are probably the basis for Harrington's statement that the blood flows now forward, now backward in the subneural. However, the general course of the blood flow is strictly determined, as shown by the consistent experimental and anatomical results, and no considerable or long-continued reversal or interruption of the usual current are possible except as the result of violent interference such as decapitation of the worm.

The valves in the vessels have received very meager notices heretofore. The mention of valves in the dorsal vessel by Benham has been noticed above. A recent writer [1] has mentioned the presence within the dorsal vessel of cells similar to the chloragogue cells. These are also doubtless the valves of the dorsal vessel.

Explanation of Figures.

Abbreviations: *b.w.*, body wall; *c.t*, connective tissue layer of blood vessels; *d.*, dorsal vessel; *d-i.*, dorso-intestinal vessel; *d-t.*, dorso-typhlosolar vessel; *end.*, endothelial lining of vessels; *i.v.p.*, vascular plexus of intestine; *l.n.*, lateral neural vessel; *m.*, layer of circular muscle fibers in walls of vessels; *nph.*, nephridium; *p.*, parietal vessel; *s.*, septum; *s-n.*, subneural vessel; *t.s.*, typhlosolar sinus; *v.*, ventral vessel; *va.*, valve; *v.i.*, ventro-intestinal vessel.

[1] Rice, Wm. J., "Studies in Earthworm Chloragogue," Biol. Bull., Vol. III., Nos. 1–2, 1902.